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RESEARCH ARTICLE

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Predicting the potential for spread of emerald ash borer (*Agrilus planipennis*) in Great Britain: What can we learn from other affected areas?

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Societal Impact Statement

Emerald ash borer (EAB) is thought to have arrived in North America and European Russia at least 10 years prior to detection. Despite heightened awareness that EAB could invade Great Britain (GB), detection in the early stages of establishment is difficult, and initial symptoms might be mistaken for Chalara ash dieback. Our results suggest that if partial resistance to EAB in *Fraxinus excelsior* does not significantly dampen EAB population dynamics, then EAB could establish and spread across large parts of southern England within a relatively short time period; however, further northern spread may be limited by the relatively cool climate.

Summary

- The accidental introduction of emerald ash borer (EAB) to North America and European Russia in the 1990s has resulted in an ongoing crisis with millions of ash trees damaged and killed at immense economic and social cost. Improving our understanding of how rapidly the pest might spread should it enter Great Britain (GB) plays an essential part in planning for a potential outbreak.
- Two metrics are used to investigate the potential dynamics of EAB in GB: the observed rate of spread in the North American and Russian regions; and the relationship between degree days and emergence that may determine environmental suitability and whether the life cycle is univoltine or semivoltine.
- The pest is still spreading in North America and European Russia with an overall average rate of spread between 2002 and 2018 of approximately 50 km a year. Early detection of the pest is difficult, but a similar delay in detection to that in North America would result in a costly and hard to control outbreak. Comparison of degree days between regions suggests that a semivoltine life cycle is most likely in most areas of GB but spread maybe limited by the relatively cool climate in parts of GB.
- There are several potentially important differences in the biophysical environment in GB compared with North America and European Russia. However, the speed with which it has invaded these areas highlights the need for early surveillance and mitigations to minimise human-mediated spread of this highly destructive pest.

KEYWORDS
Agrilus planipennis, degree days, emerald ash borer, epidemiology, *Fraxinus excelsior*, spatial spread

1 | INTRODUCTION

Emerald ash borer (EAB; *Agrilus planipennis*) is a member of the family Buprestidae, the jewel beetles. The genus is notable for having the largest number of species, more than 3,000 (Bellamy, 2008), of any single genus in the animal kingdom. Only a few species of *Agrilus* are considered pests, of which both EAB and *A. anxius* (bronze birch borer) currently form a potential threat to European forests. Within Great Britain (GB), there are only a few known endemic species of *Agrilus*, most notably *A. biguttatus* which, until recently, was treated as a vulnerable endemic species but is now considered a potential pest in relation to Acute Oak Decline (Brown et al., 2015).

The EAB beetle is native to north-eastern Asia where it is an endemic manageable pest controlled by several natural enemies (Wang et al., 2010). The pest was first identified in North America in 2002 and assigned the common name EAB by the Entomological Society of America to aid communication (Cappaert et al., 2005; Haack et al., 2002). Between 2003 and 2006, specimens of the beetle were also collected by several entomologists in different parts of Moscow, Russia; however, they were not officially confirmed as EAB until 2007 (Baranchikov et al., 2008; Valenta et al., 2017). Dendrochronological analysis of the outbreak in south-eastern Michigan suggests that the pest was introduced to North America somewhere between the late 1980s and early 1990s (Siegert et al., 2014) and it is possible that this is also the case for the outbreak in European Russia (Musolin et al., 2017). Current surveillance data indicate that the majority of Western Europe is free of the pest; however, EAB is widespread in European Russia increasing the risk of imminent spread across Europe (Orlova-Bienkowskaja et al., 2020).

Larval feeding creates distinctive serpentine galleries under the bark that inhibit the flow of water and nutrients between the canopy, trunk and roots, leading to canopy dieback and eventually tree death (Cappaert et al., 2005). Hundreds of millions of ash trees have been killed directly and indirectly by EAB across 35 states in the United States (United States Department of Agriculture, Animal and Plant Health Inspection Service [USDA APHIS]), five Canadian provinces (Canadian Food Inspection Agency [CFIA]) and 16 regions of European Russia (Orlova-Bienkowskaja et al., 2020) at immense economic (Kovacs et al., 2010) and social cost (Donovan et al., 2013; Kondo et al., 2017). Billions of dollars have been spent on the control of EAB, dealing with infested trees and replacement with non-host trees (Poland & McCullough, 2006), and a large literature has built up around research driven by questions on the life cycle and behaviour of the pest and strategies for disease control.

Emerald ash borer is considered the most destructive forest pest ever recorded in North America with eradication from the affected region no longer considered a viable option (Aukema et al., 2011; Herms & McCullough, 2014). Three factors that make the pest so difficult to manage are:

- EAB can establish itself without detection allowing infestations to build up to levels that are difficult to control;
- A high proportion of attacked trees die within 3–5 years;
- The beetle can disperse rapidly over large areas through a combination of active flight and human-mediated dispersal.

Once the beetle becomes established, eradication ceases to be a viable economic or practical option. However, developing strategies to slow the rate of spread, such as biological control and targeted chemical protection of host trees, enables removal of affected trees and replacement of the tree canopy to be managed more efficiently (McCullough, 2020).

Ash forests in Europe are already suffering due to the rapid spread of the fungal pathogen *Hymenoscyphus fraxineus*, which causes a disease referred to as ash dieback (ADB). A recent meta-analysis of ash mortality across Europe (Coker et al., 2019) highlighted the lack of systematic surveillance data with which to assess the impact of ADB. Coker et al. (2019) concluded that whilst some plantations are reporting up to 85% mortality from ADB, natural woodlands are currently showing lower levels of mortality. This could enable ash to recover, as seedlings of more resistant trees help to re-establish woodland populations. However, can Ash in Europe survive the combined attack of EAB and ADB?

A key question is how much European countries should invest in pre-emptive strategies, such as surveillance and attaining approval for chemical and biological control agents, to mitigate against the arrival and establishment of EAB. The answer depends on a complex interaction of climatic suitability, the genetic profile of European ash, host health, host density, and the influence of human behaviour and native predators and parasites on EAB dynamics. Ash is the second most abundant tree species in GB, where it is a common feature in hedgerows and woodland (Maskell et al., 2013) presenting a highly connected landscape through which EAB could disperse. However, a potentially important difference between North America, Russia and GB is the distribution of particular ash species. The predominant species in GB, *Fraxinus excelsior* (European Ash), is rarely planted in North America and, whilst *F. excelsior* is native to European Russia, the non-native *F. pennsylvanica*, introduced from North America, is the predominant species in many cities and along highways in Russia (Baranchikov et al., 2014; Musolin et al., 2017). Evidence on the relative impact of EAB on *F. excelsior* versus *F. pennsylvanica* in European Russia is difficult to interpret due to lack of reported systematic longitudinal studies. Whilst there is some evidence that *F. excelsior* appears to be more resistant to damage by EAB than both *F. pennsylvanica* (Orlova-Bienkowskaja et al., 2020; Straw et al., 2013) and another native American ash, *F. nigra* (Showalter et al., 2020), there is also clear evidence from all studies that the resistance is only partial. Examination of ash species in the main botanical garden of the Russian Academy of Sciences in Moscow found 70% (45 out of 64) of specimens of *F. excelsior* were dead or dying and had evidence of EAB infestation compared to 89% (48 out of 54) of specimens of *F. pennsylvanica* (Baranchikov et al., 2014).

A potentially important factor that could mitigate the impact of EAB in GB is the duration of the life cycle of EAB which varies between 1 and 2 years (Herms & McCullough, 2014). The precise mechanisms driving the duration of the life cycle are unclear with climate, larval population density, host subspecies, and host health all apparent contributing factors (Cappaert et al., 2005; Herms & McCullough, 2014; Jones et al., 2019; Orlova-Bienkowskaja & Bieńkowski, 2016; Siegert et al., 2010; Tluczek et al., 2011). However, in general, in warm climates, the life cycle is univoltine whilst in cooler climates a 2-year life cycle predominates. Between the two extremes, the life cycle is less predictable and can vary within cohorts and with annual temperature fluctuations (Jones et al., 2019; Orlova-Bienkowskaja & Bieńkowski, 2016).

In New York, where a mixture of 1 and 2-year life cycles has been observed, two peaks in third/fourth instar larvae were recorded with the first peak attributed to EAB that overwintered as early instar larvae and the second peak arising from eggs laid that season (Jones et al., 2019). Despite the early first peak, and adequate degree day accumulation within the same season, neither pupae nor pharate adults were detected after early July supporting the hypothesis that EAB needs to overwinter in the prepupal stage to complete the life cycle (Jones et al., 2019). It is likely that compulsory overwintering as prepupae leads to the observed synchronisation of adult emergence, with the majority of emergence within local populations occurring within a 4- to 6-week period (Duart, 2013; Jones et al., 2019).

A range of mathematical models for the spatial spread of EAB at local and regional scales have been developed to investigate pest dynamics and inform policy in North America (Siegert et al., 2015). Early models for the spatial spread of EAB highlighted the role of anthropogenic spread and the need for effective firewood quarantines (BenDor et al., 2006; Muirhead et al., 2006; Iverson et al., 2010; Prasad et al., 2010). Economic analyses, using an exponential dispersion kernel to simulate the long-distance spread of the pest, demonstrated the importance of investing in surveillance measures for rapid identifications of new incursions of EAB and in control measures to slow, and where possible eradicate, the beetle (Kovacs et al., 2010). As more data have become available on the dynamics of EAB and the host landscape, models have been used to explore options for slowing down the spread of EAB given that eradication is no longer feasible (McCullough & Mercader, 2012; Mercader et al., 2011, 2016; Kovacs et al., 2014; Lyttek et al., 2019). Refined predictions of the rate and direction of spatial spread from new outbreaks remain difficult due to uncertainties over the drivers for EAB short and long-distance flight, variation in human-mediated spread and the impact of landscape management on pest dynamics (Siegert et al., 2015). In the event of identification of an established population of EAB in GB, the most urgent question would be "How far has it spread and how can we eradicate the pest?" Uncertainties over the impact of different ash species and other local variables typical of the GB setting on EAB dynamics mean that, in the absence of a known outbreak area from which to estimate local parameters, adapting existing models to obtain more precise predictions of spread would be challenging. We have therefore adopted a simpler approach of estimating the potential extent of infestation, encompassing multiple satellite outbreaks, if EAB were to establish in GB.

In this paper, we consider two simple metrics to gauge the potential for EAB establishment and spread across GB. In the first part of our analysis, we compare the observed rate of spread of EAB across the United States, Canada and Russia using national level records. In the second part, we consider environmental suitability for EAB establishment and spread by comparing predicted dates of early and peak adult emergence in known infested areas, based on a literature review of reported degree days to emergence, with predicted emergence dates in GB. We ask whether the climate in GB provides a suitable environment for EAB and if so whether we would expect EAB in GB to be univoltine or semivoltine.

Finally, we combine these analyses to consider the potential spatial spread of EAB at a national scale if accidentally imported into either central England or the Southeast of England and (i) it was detected soon after the initial infestation became established; or (ii) there was a period of 5–10 years before its presence were detected, which is analogous to delays in North America. The purpose of this analysis is to inform national strategies for increasing surveillance and implementing control measures should an outbreak be detected in GB and to highlight the need for investment in pre-emptive surveillance and control strategies.

2 | MATERIALS AND METHODS

2.1 | Estimation of the rate of spread of EAB

In this analysis, we take a global overview of the spread rate, focussing on the combined impact of short and long-distance dispersal in the existing areas of infestation, to investigate the potential speed at which EAB could invade GB.

National data on the presence of EAB by year were obtained for the United States, Canada and European Russia (Figure 1). The dataset for the United States, compiled by USDA APHIS, consists of county level records by year of first positive identification (Ward et al., 2020). The dataset for Canada, compiled by CFIA and supplied under the Open Government Licence—Canada (later years were manually extracted from individual outbreak reports; Canadian Food Inspection Agency, 2020), consists of georeferenced point locations by year of first positive identification. Geolocated data on the annual reported locations of EAB in European Russia were extracted from Orlova-Bienkowskaja et al. (2020). These data comprise both ad hoc reports from the literature and from epidemiological surveys. The first reported regional survey for the pest was conducted

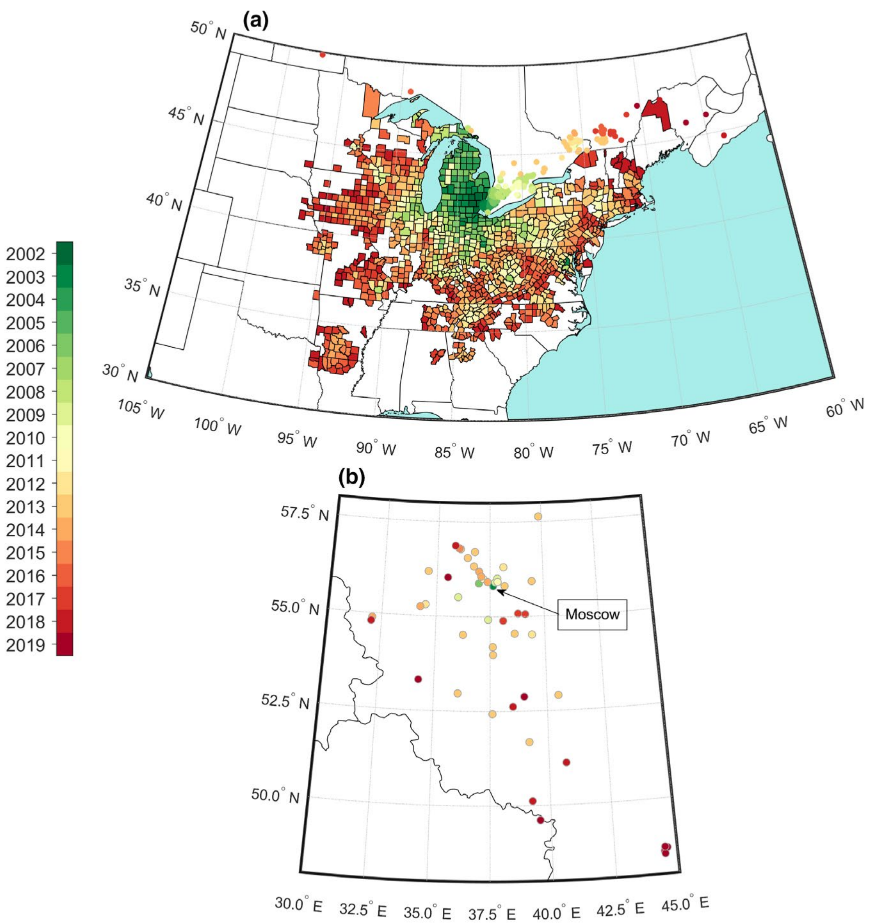

FIGURE 1 Reported spread of emerald ash borer in (a) North America and (b) European Russia by year of first positive identification. Data for the United States, compiled by the United States Department of Agriculture, Animal and Plant Health Inspection Service (Ward et al., 2020), consist of county level reports up to 31 December 2018. Data for Canada, compiled by the Canadian Food Inspection Agency and supplied under the Open Government Licence—Canada, and for European Russia, extracted from Orlova-Bienkowskaja et al. (2020), consists of point locations up to 2019

in 2009 covering a radius of approximately 150 km from Moscow (Baranchikov et al., 2008). The degree of annual surveillance for the pest varies with no new data reported in the literature in some years.

Emerald Ash Borer was first identified in North America in 2002. During that year the presence of the pest was confirmed in six counties in Southeast Michigan (Macomb, Livingston, Monroe, Oakland, Washtenaw and Wayne) and in Essex County, Ontario (Haack et al., 2002). Subsequent dendrochronological reconstruction of the initial outbreak area points towards the outbreak originating in the suburb of Canton in the north west of Wayne County (estimated as 42.31°N, 83.49°W) in 1997 (Siegert et al., 2014). We assume that this site forms the epicentre of the outbreaks both in the United States and Canada.

Emerald ash borer was officially confirmed in Moscow, where the dominant ash species is *F. pennsylvanica*, in 2007 by which time it was already well established across the city (Baranchikov et al., 2008) and we assume that this is the epicentre for the outbreak in European Russia (estimated as 55.81°N, 37.64°E).

For each dataset, the Euclidean distance between the centroid of each county or point location, as applicable, and the country specific epicentre was calculated and converted to kilometres. The rate of spread of EAB was estimated by fitting linear and exponential functions to the data with the intercept fixed at the maximum distance from the epicentre that cases were reported in the first year that the pest was identified. The most appropriate function to describe each dataset was selected based on the minimum r^2 value, where r^2 is a measure of how well the data are explained by the regression. Direct comparison of r^2 values between the datasets is not possible because of differences in observation numbers and protocols for data collection (all known occurrences in North America vs. targeted surveys in European Russia).

2.2 | Impact of climate on the duration of the life cycle of EAB

We compare accumulated degree days between the known infested areas in North America and European Russia, with accumulated degrees days across Europe focussing on GB.

Reported values of the relationship between degree days, first and peak emergence vary. This variation can, in part, be attributed to differences in how degree days are calculated (average value formula vs. sine wave methods, base temperature 13.5°C or 10°C); how emergence is measured (direct observation, indirect observation via recording exit holes, capture of flying adults in traps); and, frequency of observations (see, for example, Brown-Rytlewski & Wilson, 2004; Cappaert et al., 2005; Duart, 2013; Jones et al., 2019; Lyons & Jones, 2005; Poland et al., 2011) but may also be attributed to differences in EAB population density, host health and other climatic factors. For the purposes of this exploratory analysis, we selected two threshold values that aim to capture the range of values reported in the literature: 230°C DD_{10}, which is consistent with early emergence in all studies (and often quoted as the threshold for emergence on the basis of a study by Brown-Rytlewski & Wilson, 2004) and 500°C DD_{10}, which is consistently within the early to main emergence period for EAB. In regions where these thresholds are met early in the year, the EAB lifecycle is predominantly univoltine. In cooler regions, where these thresholds are met later in the year, a 2-year lifecycle predominates. Regions in which these thresholds are not met within a calendar year or are met late in the year are unlikely to provide a suitable environment for EAB to establish.

Accumulated degree days were calculated from 1st of January each year using the modified sine-wave method (Baskerville & Emin, 1969) assuming a base temperature of 10°C, below which no development occurs (Brown-Rytlewski & Wilson, 2004). The start date of 1st of January is commonly used for the calculation of accumulated degree days in phenological models of insect development in the Northern Hemisphere as it provides a convenient date within which insects are in a state of quiescence. Weather data for 2007–2018 were obtained from ERA5-Land (Copernicus Climate Change Service (C3S; 2019): C3S ERA5-Land reanalysis. Copernicus Climate Change Service, date of access: 14 February 2020;). ERA5-Land is a reanalysis dataset that provides a consistent global dataset by combining weather observations with model data. ERA5-Land is a calculation of land variables over several decades at an improved resolution compared with ERA5 (0.1° × 0.1° vs. 0.25° × 0.25°). The temporal frequency of the output is hourly, and the fields are masked for all oceans.

2.3 | Potential spread of EAB across GB

Two hypothetical epicentres for the introduction of EAB into GB were selected to contextualise the invasion of the pest in GB if the beetle were to spread at rates equivalent to those in North America conditioned upon the availability of sufficient accumulated degree days to permit insect development. The starting points: (i) Dover, on the South East coast of England and; (ii) Birmingham, in central England; were selected to represent potential points of entry via shipping or direct transport. We start our illustration from the first year in which EAB causes tree death and define this as year zero. Following Ward et al. (2020) we assume that the first tree death marks the end of the establishment phase of the pest during which Ward et al. (2020) suggest there is minimal spread.

Dendrochronological reconstruction of the outbreak in North America suggests that the first EAB induced tree death occurred in 1997 (Siegert et al., 2014), 5 years prior to the commencement of data recording. In 2002, the pest was detected 102 km from the epicentre estimated by Siegert et al. (2014). This implies an average rate of spread, allowing for satellite jumps, of approximately 20 km/year during this 5-year period. Thereafter, we use the average estimated rate of spread from the combined North American data (see results: 47 km/year).

The estimated extents of radial spread calculated from the cumulative expansion rate were plotted around the two hypothetical points of entry and overlaid on threshold degree day map data for GB from 2007 to 2018. These years are selected for illustrative purposes to highlight annual variation in the date at which different regions reach 230°C DD_{10} and 500°C DD_{10}. We assume a cut-off for early emergence of the 1st of September for EAB to be able to establish in a region and suggest that if the pest is introduced to an area that does not reach this cut-off, then it is unlikely to establish in that area. The September cut-off is based on: the need for adults to feed on ash leaves for 5–7 days before mating and a further 5–7 days before oviposition (Cappaert et al., 2005); a reported early flight period occurring in May or June elsewhere; staggered emergence of adult beetles (Wang et al., 2010); and observed cessation of flight between early August and early September at a range of latitudes (Brown-Rytlewski & Wilson, 2004; Cappaert et al., 2005; Duart, 2013; Lyons & Jones, 2005; Orlova-Bienkowskaja & Bieńkowski, 2016). We further assume that if the climate at any location is suitable when the wavefront reaches it, then onward spread of the pest can occur from these locations in future years even if the climate is not suitable in some years.

All plotting and analyses were conducted in MATLAB® 2020b using in-built functions, user contributed functions Violinplot (Bechtold, 2016) and ColorBrewer (Cobeldick, 2020) and The Climate Data Toolbox (Greene et al., 2019).

3 | RESULTS

3.1 | Spatial spread of EAB in current outbreak regions

Emerald ash borer has continued to spread through both North America and European Russia (Figure 1). In North America, spread to the west and north is limited in some regions by a lack of suitable host. In addition to local dispersal of the beetle via both active dispersal and anthropogenic spread, a number of human-mediated extreme long-distance jumps, such as the jump from Michigan to Maryland in 2003; and, the identification of an outbreak in Colorado in 2013 over 600 miles (equivalent to the entire length of GB) from the nearest known infested area (Alexander et al., 2019), highlight the risk of long-distance dispersal via infested saplings and firewood despite measures to restrict spread from known infested regions. The distance of new infestations from the epicentre was better captured by a linear function for the United States (linear: $r^2 = .48$ vs. exponential: $r^2 = .27$; Figure 2a); however, there was little to distinguish between the r^2 values for a linear and an exponential model for Canada (linear: $r^2 = .70$ vs. exponential: $r^2 = .73$). The exponential model provides a better visual fit to the data for Canada (Figure 2b) particularly in the early years—the initial slower rate of expansion might in part be explained by the natural barrier to spread provided by the Great Lakes. In 2002, the year in which EAB was identified as the cause of ash decline in North America; the pest had already

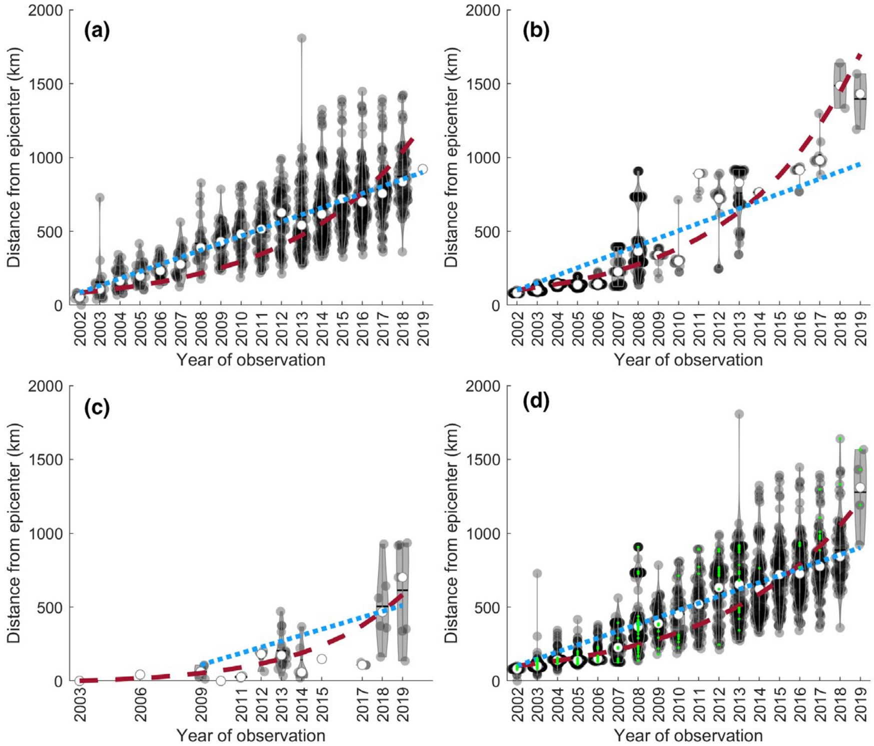

FIGURE 2 Relationship between reported year of infestation by emerald ash borer and distance from the reported epicentre of the outbreaks in (a) the United States, (b) Canada, (c) European Russia and (d) combined data for North America. The intercept for the regression lines was fixed for each country as the furthest distance recorded from the epicentre in 2002 except for the linear fit for European Russia where the data were fitted from 2009 onwards. The regression lines for year (y) against distance from epicentre in km (x; $\pm SE$) are (a) the United States—linear fit: $y = 83.6 + 48(\pm 0.5)x$; exponential fit: $y = 83.6e^{0.158(\pm 0.001)x}$; (b) Canada—linear fit: $y = 102 + 50.2(\pm 0.8)x$; exponential fit: $y = 102\left(e^{0.166(\pm 0.001)x}\right)$; (c) European Russia—linear fit starting from furthest extent from Moscow in 2009 and only including years where there was active surveillance: $y = 107.5 + 40.4(\pm 5.1)x$; exponential fit from 2003 with zero intercept: $y = 20.5(\pm 16.3)\left(e^{0.21(\pm 0.05)} - 1\right)$; (d) combined data from North America—linear fit: $y = 102 + 47.1(\pm 0.4)x$; exponential fit: $y = 102\left(e^{0.146(\pm 0.001)x}\right)$. Violin plots show the median (white circle) and individual (grey circles—note these appear black where multiple locations are a similar distance from the epicentre) recorded distances from the epicentre each year. The green circles on subplot (d) highlight the data points for Canada. Data for the United States were compiled by the United States Department of Agriculture, Animal and Plant Health Inspection Service (Ward et al., 2020). Data for Canada were compiled by the Canadian Food Inspection Agency and supplied under the Open Government Licence—Canada. Data for European Russia were extracted from Orlova-Bienkowskaja et al. (2020)

extended at least 80 km from the assumed epicentre into Michigan and 100 km into Canada. Fitting a linear model to each set of data gives an estimated expansion rate from the edge of the infestation in 2002 of 48 km (95% CI: 47–49) per year for the United States and 50.2 km (95% CI: 48.5–51.8) per year for Canada. Combining the two data sets gives a slightly lower estimated expansion rate of 47.1 km (95% CI: 46.3–47.9) per year since the intercept is set at the furthest point from the epicentre of the two distances (102 km; cf Figure 2a,b,d). The combined expansion rate is used to infer the spread in GB (see Section 3.3).

The spread of EAB in European Russia has tended towards the south and west of the country (Figure 1b). Recent surveys indicate that EAB is close to the border with the Ukraine and Belarus with infestation identified in trees over 900 km from Moscow (Orlova-Bienkowskaja et al., 2020). The distance of new infestations from the epicentre of the outbreak in European Russia was best captured by an exponential function (linear: $r^2 = .31$ vs. exponential: $r^2 = .48$; Figure 2c); however, the absence of annual country wide systematic surveillance leads to low confidence in this result. Reanalysing using a linear function starting in 2009 with intercept given by the maximum extent in 2009, estimated to be 107 km, and only using data from 2012–14 and 2018–19 gives an average rate of spread, 40.4 km (95% CI: 30–50.7, $r^2 = .42$) per year which is consistent with that observed in North America; however, it is important to note the potential impact of missing data when comparing the data sets.

3.2 | Impact of climate on the duration of the life cycle of EAB

Based on a threshold degree day accumulation of 230°C DD_{10} for early emergence of EAB, and averaging over 10 years of weather data (2008–2018), we would expect to see emergence of adult beetles in the most northerly known infested areas of Russia to commence in June with an earlier start to emergence elsewhere in the country (Figure 3c). Similarly, in the United States predicted dates

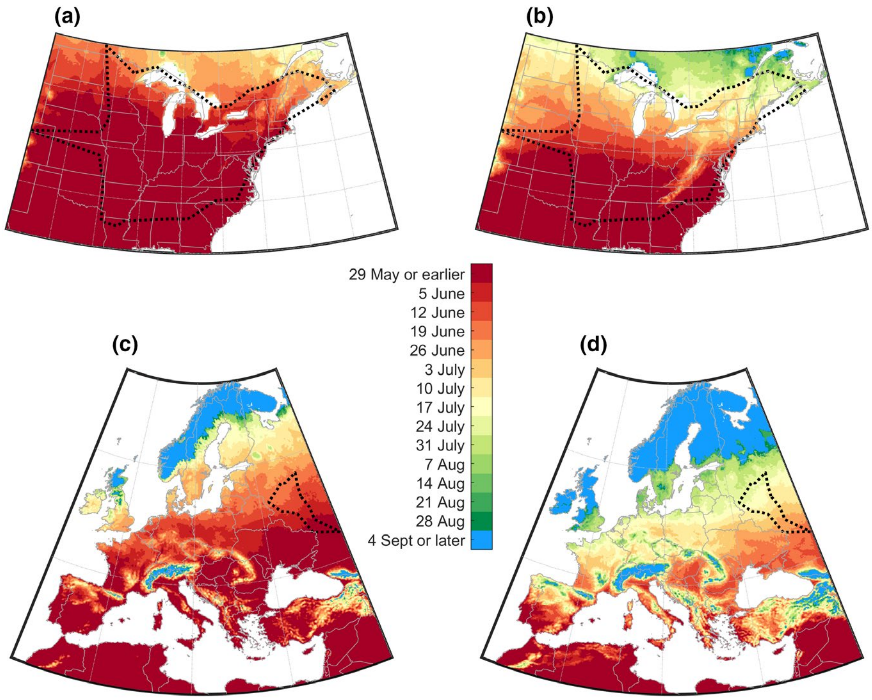

FIGURE 3 Comparison of average week (using ERA-5 Land data from 2008–2018) to reach degree day thresholds in the known invaded regions and in areas where emerald ash borer is not known to be present (to 31 December 2018 for the United States and to 2019 elsewhere). North America (a) 230 DD_{10}, (b) 500 DD_{10}; and, Europe (c) 230 DD_{10}, (d) 500 DD_{10}. The dotted outlines give the boundaries around all recorded occurrences of emerald ash borer in North America and European Russia. The dates on the colour scale are the first date on which the degree day threshold is reached

for early emergence in the majority of infested areas are June or earlier (Figure 3a), which is consistent with published reports (Herms & McCullough, 2014; Jones et al., 2019; Orlova-Bienkowskaja & Bieńkowski, 2016). In parts of Canada, first emergence is predicted to occur in the first few weeks of July (Figure 3a). Despite mild winters, only the southeast of GB is expected to accumulate 230°C DD_{10} by the end of June with predicted earliest emergence for the majority of central England and Wales in July (Figure 3c). Note, however, the 10-year average hides annual variation and in more recent years the threshold has been reached in June across a larger area of England and Wales (Figures 4 and 5). In parts of Northern England and most of Scotland, the threshold is not reached until late summer or early autumn, so it is possible that these areas are not conducive to establishment of EAB unless the species is able to adapt (Figure 2c). The relatively late emergence in GB suggests that we would expect a 2-year life cycle where the pest is able to establish. Accumulation to 500°C DD_{10} is slower in the majority of GB compared with even the most northerly infested areas of Russia and Canada (cf Figure 3b,d) and is reached after leaf-fall in many parts of Northern England and Wales, and never reached in high lying areas of Scotland.

Extending this exploration further across Europe, we see that although much of southern Europe reaches the 230°C DD_{10} threshold by early May (Figure 3c), degree day accumulation to 500°C DD_{10} over the summer is relatively slow (Figure 3d), with calculated dates similar to those in European Russia and Canada. This suggests that if EAB phenology is unaffected by *Fraxinus* species, we would see a 2-year lifecycle in many regions, a mixture between 1- and 2-year lifecycle as we move south and a predominantly 1-year life cycle only in the most southern parts of Europe. The most Northern parts of Europe do not reach the 230°C DD_{10} within the hypothesised viable emergence period (Figure 3c).

3.3 | Potential spread of EAB across GB

If an EAB introduction is not intercepted on entry to GB and the pest is able to start breeding, then there is a high chance that, despite increased awareness of EAB in GB, the presence of the pest will be missed until at least the end of the establishment phase. Assuming an initial radial expansion of 20 km, after the end of the establishment phase, gives a potential area at detection of over 1,000 km^2 to search for satellite infestations originating from a single site of introduction (Figure 4, Year 1) with each year delay leading to an increased search area (Figure 4).

The rate of expansion of the range of EAB from 2002 onwards was initially slower in Canada than North America (cf Figure 2a,b). Whether this is due to the natural barrier to spread, differences in efficacy of quarantine or a slower local invasion of EAB, due to a 2-year lifecycle reducing the probability of human mediated spread, is unclear. However, by the time the pest was identified as the cause of ash decline in North America, the estimated distance from the epicentre was similar for both countries (Figures 1a and 2a,b). This would be equivalent to the first identification of EAB occurring 5 years after the end of the establishment phase for the illustrative GB outbreaks highlighting the relatively small size of GB compared with North America (Figure 4, Year 5). If the area encompassing, all EAB infestations were to expand at the same average rate in GB as estimated for North America from 5 years after the end of the establishment phase onwards (47 km/year), the pest could spread across most of England and Wales within 10 years of the establishment of the initial infestation (Figure 5). Dispersal to the north and west is likely to be limited by climate with very late emergence potentially resulting in a lack of food for emerging beetles; however, in 2017 and 2018 (Years 10 and 11, Figure 5), the degree day thresholds were

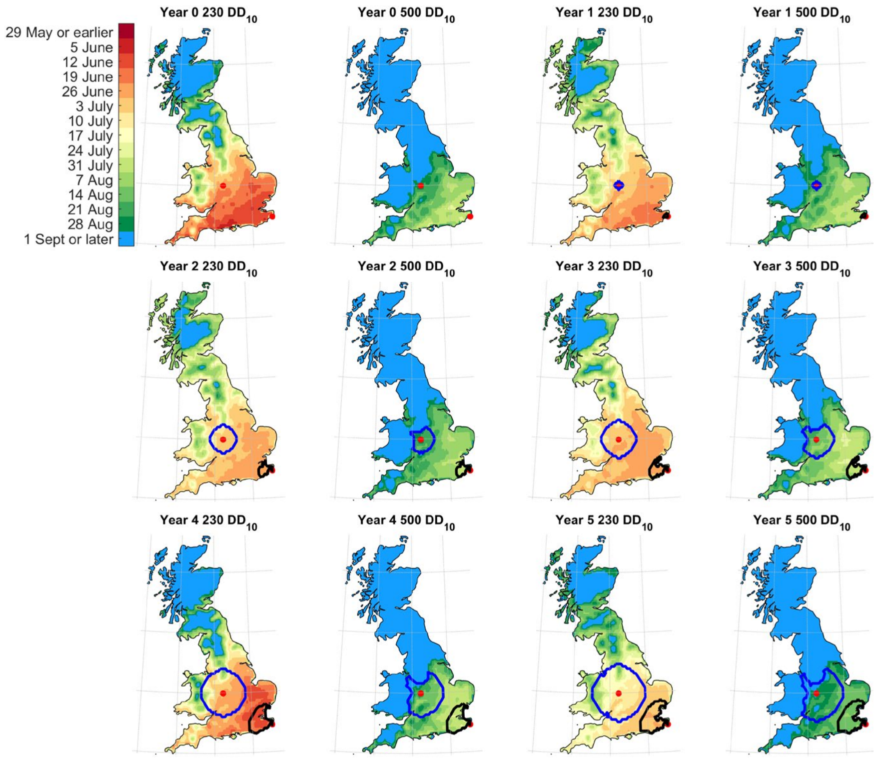

FIGURE 4 Mapping the potential spread of emerald ash borer in Great Britain (GB) following the end of the establishment phase if the beetle spreads at a similar rate to that observed in North America. Year 0 represents the first year in which trees die. The average spread rate up to Year 5 is estimated to be 20 km/year. Introduction points are for illustration only—at the time of publication emerald ash borer has not been detected in Great Britain. Annual threshold maps (early emergence 230 DD_{10}; mid-peak emergence 500 DD_{10}) from 2007 to 2012 for GB are used to illustrate annual variation in threshold date. The raw data, which has a resolution of 0.1° × 0.1°, are interpolated for visual purposes. The average extent of infestation originating from two illustrative epicentres each year is determined by combining the average rate of spread from the outer edge of infestation in the previous year with the original threshold maps for two scenarios: either (i) 230 DD_{10} or (ii) 500 DD_{10} must be reached by 1st of September for the insect to successfully invade a grid cell. The epicentres are chosen to capture two potential scenarios: one in central England (blue boundary line) and the other in the southeast of England (black boundary line). Boundary lines are drawn using an in-built MATLAB® algorithm to encompass the centroids of all infested locations

met earlier in many parts of GB which would have enabled emergence and onward dispersal of the pest if present.

4 | DISCUSSION

Long distance dispersal of pests and pathogens through international trade and travel can have a devastating effect on native tree populations with delayed recognition and identification of the threat a common thread in subsequent enquiries. The impact of many pests and pathogens increases as they move out of their native range, where hosts may have developed some level of resistance attributed to a coevolution, to an area of evolutionary naïve hosts (Gandhi & Herms, 2010). Hence, there is often little known or published about the pest prior to invasion. It is likely that EAB was present in North America for at least 10 years prior to the first beetles being reared and identified (Siegert et al., 2014) at which point, after extensive efforts to identify the pest, researchers were only able to identify two papers from China that provided some insight to the life cycle of EAB (Haack et al., 2002). Since then billions of dollars have been poured into research and control of EAB and >800 papers published. However, there are still areas of uncertainty including the precise mechanisms controlling the life cycle of the pest and driving active dispersal of the pest.

Efforts to first eradicate, then quarantine, EAB have failed to stop the pest from spreading in North America and new areas of infestation continue to be identified. An important issue with controlling EAB is the long period of cryptic infestation whereby in the first year of colonisation eggs are laid deep in the bark crevices high up in the canopy with emergence holes easily missed (Haack et al., 2002) allowing the pest to replicate and disperse into the wider environment over two or three generations without detection. As a result, even apparently isolated outbreaks, such as the long-distance spread to Colorado (Alexander et al., 2019), are too costly to stamp out.

Much of Europe is currently thought to be free of EAB but, having witnessed the devastation and cost of dealing with the pest in North America, European countries, including GB, are concerned that accidental import could lead to similar destruction of European Ash trees which are already suffering from widespread infection by the fugal pathogen *H. fraxineus*, the causal organism of ADB. This

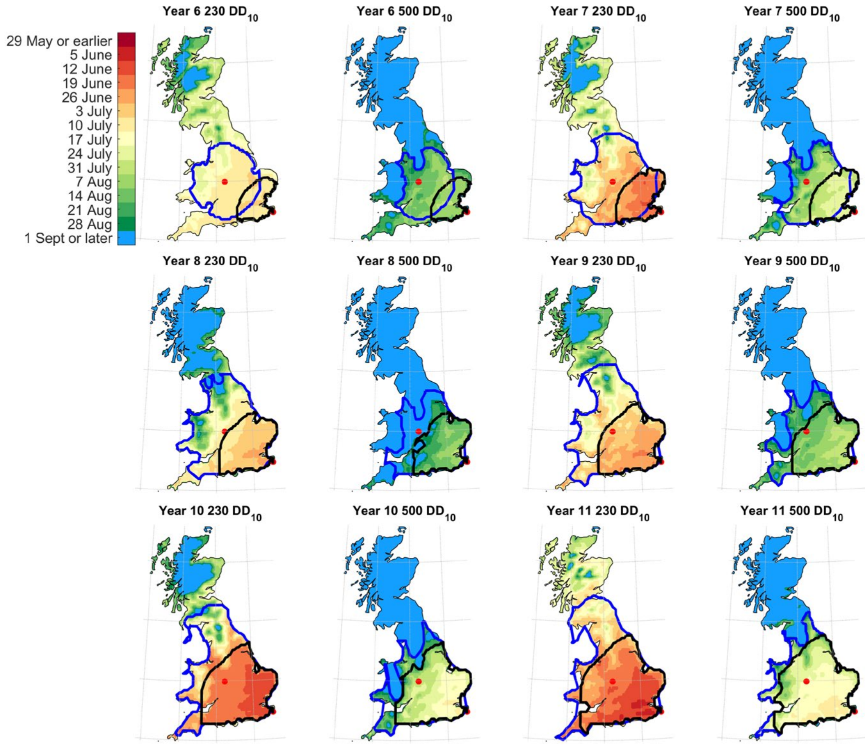

FIGURE 5 Mapping the potential spread of EAB in Great Britain (GB) from 6 years after the end of the establishment phase (the year in which the first trees die which we define as Year 0) if the beetle continued to spread at a similar rate to that observed in North America. From Year 5 onwards, we apply an average spread rate of 47 km/year as estimated from linear regression of the North American data. Introduction points are for illustration only—at the time of publication emerald ash borer has not been detected in Great Britain. Annual threshold maps (early emergence 230 DD_{10}; mid-peak emergence 500 DD_{10}) from 2013 to 2018 for GB are used to illustrate annual variation in threshold date. The raw data, which has a resolution of 0.1° × 0.1°, are interpolated for visual purposes. The average extent of infestation originating from two illustrative epicentres each year is determined by combining the average rate of spread from the outer edge of infestation in the previous year with the original threshold maps for two scenarios: either (i) 230 DD_{10} or (ii) 500 DD_{10} must be reached by 1st of September for the insect to successfully invade a grid cell. The epicentres are chosen to capture two potential scenarios: one in central England (blue boundary line) and the other in the southeast of England (black boundary line). Boundary lines are drawn using an in-built MATLAB® algorithm to encompass the centroids of all infested locations

paper focused on exploring the potential dynamics of EAB in GB using data on the spread of the pest in North America and European Russia, as a precursor to developing a model for the spread of EAB in GB. Our results concern the relationship between degree day accumulation and EAB emergence and the speed at which EAB could spread across the GB landscape. We find that some areas of GB may be unsuitable for EAB establishment due to low-temperature accumulation across the year which may result in beetle emergence too late in the season or not at all. However, where EAB is able to establish the pest could rapidly spread over a large area causing extensive damage to the host landscape.

Whilst dendrochronological analysis suggests that local expansion of colonies through active flight is approximately 4 km/year (Siegert et al., 2014), the apparent ease with which the pest is dispersed through anthropogenic routes means that the true annual extent of spread is much larger. During the active flight stage of EAB, short distance dispersal occurs via gravid females seeking suitable hosts, but it has also been suggested that long-distance dispersal may occur via beetles hitchhiking on clothing, vehicles (Buck & Marshall, 2008) and/or train carriages (Short et al., 2020). However, the bulk of long-distance dispersal is likely to occur during other lifecycle stages through transport of contaminated wood and saplings. Teasing out the spread rates for each mechanism of spread is complicated by the wide range over which human-mediated spread can occur: from local disturbances, through activity such as pruning and firewood storage; to long distance dispersal via movement on vehicles, saplings, timber and firewood. For EAB, as with many other insects, there is further complication as flight and choice of location for oviposition are likely to be affected by intraspecific competition, host preference and host availability. By combining the results of flight mill studies with measurements of free speeds, Taylor et al. (2010) concluded that some EAB females are capable of flying >20 km/day potentially enabling much longer distance spread of EAB via active flight. Overlaying the estimated average rate of spread of EAB in North America highlights both the potential for silent spread prior to identification of the pest and the speed at which the pest could spread in GB.

A valid criticism of imposing observed spread rates in other regions on to GB is the potential for anthropogenic spread in GB versus North America and European Russia. A key feature of the early spread of EAB in North America was the transportation of contaminated wood for recreational use such as camping trips. A study of firewood bundles purchased from retailers selling direct to the public in the Rocky Mountains, USA found that over 50% of the bundles contained at least one species of insect with some larvae taking 18 months to emerge from the firewood (Jacobi et al., 2012). Orlova-Bienkowskaja and Bieńkowski (2018) argue that the spread of EAB through transport of firewood is less likely in Russia with long-distance dispersal mainly driven by other processes such as adults hitchhiking on vehicles (Orlova-Bienkowskaja & Bieńkowski, 2018; Short et al., 2020; Straw et al., 2013). Hitchhiking is much harder to control; however, given the current extent of spread in Russia, it seems likely that at least some dispersal occurred via infested wood or saplings. In the United Kingdom, many campsites do not allow open fires, and those that do often supply firewood to campers; however, one potential source of human mediated spread of infested wood is through the use as a heating fuel. A survey of domestic wood use in the United Kingdom found 7.5% of households use wood fuel for some of their heating (Waters, 2016).

Comparison of degree day accumulation between currently infested areas and GB implies that EAB may struggle to synchronise emergence with food availability in most of GB and where the beetle is able to survive, we might expect a semivoltine life cycle. There are several potentially important differences in the biophysical environment that could affect this conclusion. GB winters are mild and so may be more conducive to a longer development period enabling completion of life stages into late autumn; however, this effect may be restricted by photoperiod which can also affect the timing of winter dormancy (Saunders, 2020); many of our trees are weakened by ADB with unknown impact on EAB behaviour and development (Dearborn et al., 2018; Showalter et al., 2020); the spatial distribution, mix with other species, and planting density may impact active flight distances; and parasitoids already present in the environment may attack EAB (Bauer et al., 2015). In addition, based on the variation in reported degree days at emergence and at peak flight activity, the link between degree day accumulation and behaviour does not appear to be as strong as reported for many other species. The relatively warm climate in the southeast of England compared with the rest of GB offers a potential region in which the pest could establish with a 2-year life cycle which is likely to slow down the population growth rate (Mercader et al., 2011) but conversely may delay detection of newly infested areas, allowing larger scale undetected spread of the pest.

A key focus of ongoing research is the potential protection provided by the dominance of *F. excelsior* in GB. Experimental studies have demonstrated partial resistance of *F. excelsior* to EAB under laboratory conditions (Showalter et al., 2020). In the field, this resistance may make it harder for the pest to establish and slow population growth, thereby providing a longer window for control of new outbreaks. A recent survey of 500 *F. excelsior* trees in two areas of forest, situated 25 km apart and within the known range of EAB in European Russia, found no signs of EAB infestation which may indicate that natural forest stands of *F. excelsior* are resistant to EAB invasion (Orlova-Bienkowskaja et al., 2020). However, more detailed surveys, including the use of traps, are required to investigate whether this is due to lack of opportunity to invade, preference for *F. pennsylvanica* where choice is available or resistance of *F. excelsior* to invasion.

If European countries intend to pursue a policy of eradication for any entry of EAB, then they need proactive investment in intensive early surveillance and pre-emptive implementation of measures that limit the opportunity for human mediated spread should the pest arrive. Passive surveillance without the use of active trapping is likely to miss the early stages of infestation and even when significant signs of dieback occur, the widespread presence of ADB could lead to delayed investigation on the assumption that the cause is ADB. If the pest can adapt to the UK climate, then examples from Russia and America show that rapid spread across the United Kingdom once the pest is established is inevitable and so research also needs to focus on options for biocontrol in the United Kingdom to limit the damage that EAB has on UK ash.

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AUTHOR CONTRIBUTION

CRW planned and carried out the project with advice from CAG. CRW and CAG wrote the manuscript. TM sourced and extracted the climate data.

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REFERENCES

Alexander, K., Truslove, M., Davis, R., Stephens, S., & Zentz, R. (2019). A collaborative approach to preparing for and reacting to emerald ash borer: A case study from Colorado. *Forestry*, *93*, 239–253. https://doi.org/10.1093/forestry/cpz070

Aukema, J. E., Leung, B., Kovacs, K., Chivers, C., Britton, K. O., Englin, J., Frankel, S. J., Haight, R. G., Holmes, T. P., Liebhold, A. M., McCullough, D. G., & Von Holle, B. (2011). Economic impacts of non-native forest insects in the continental United States. *PLoS One*, *6*, 1–7. https://doi.org/10.1371/journal.pone.0024587

Baranchikov, Y., Mozolevskaya, E., Yurchenko, G., & Kenis, M. (2008). Occurrence of the emerald ash borer, *Agrilus planipennis*, in Russia and its potential impact on European forestry. *EPPO Bull*, *38*, 233–238. https://doi.org/10.1111/j.1365-2338.2008.01210.x

Baranchikov, Y. N., Seraya, L. G., & Grinash, M. N. (2014). All European ash species are susceptible to emerald ash borer *Agrilus planipennis* Fairmaire (Coleoptera: Buprestidae) - a Far Eastern Invader. *Siberian Journal of Forest Science*, *6*, 80–85. https://sibran.ru/en/journals/issue.php?ID=162986&ARTICLE_ID=162993

Baskerville, G., & Emin, P. (1969). Rapid estimation of heat accumulation from maximum and minimum temperatures. *Ecology*, *50*, 514–517. https://doi.org/10.2307/1933912

Bauer, L. S., Duan, J. J., Gould, J. R., & Van Driesche, R. (2015). Progress in the classical biological control of *Agrilus planipennis* Fairmaire (Coleoptera: Buprestidae) in North America. *The Canadian Entomologist*, *147*(3), 300–317. https://doi.org/10.4039/tce.2015.18

Bechtold, B. (2016) Violinplot. https://github.com/bastibe/Violinplot-Matlab. Accessed 11 Nov 2020.

Bellamy, C. L. (2008). *A world catalogue and bibliography of the jewel beetles (Coleoptera, Buprestoidea)*. Pensoft.

BenDor, T. K., Metcalf, S. S., Fontenot, L. E., Sangunett, B., & Hannon, B. (2006). Modeling the spread of the Emerald Ash Borer. *Ecological Modelling*, *197*(1–2), 221–236. https://doi.org/10.1016/j.ecolmodel.2006.03.003

Brown, N., Inward, D. J. G., Jeger, M., & Denman, S. (2015). A review of *Agrilus biguttatus* in UK forests and its relationship with acute oak decline. *Forestry*, *88*, 53–63. https://doi.org/10.1093/forestry/cpu039

Brown-Rytlewski, D., & Wilson, M. A. (2004). Tracking the emergence of emerald ash borer adults. In V. Mastro & R. Reardon (Eds.), *Emerald ash borer research and technology development meeting*, (pp. 13–14). USDA Forest Service publication FHTET-2004-15.

Buck, J., & Marshall, J. (2008). Hitchhiking as a secondary dispersal pathway for adult emerald ash borer. *Great Lakes Entomologist*, *41*, 197–199.

Canadian Food Inspection Agency. (2020). *Emerald ash borer – Latest information*. https://www.inspection.gc.ca/plant-health/plant-pests-invasive-species/insects/emerald-ash-borer/latest-information/eng/1337287614593/1337287715022. Accessed 27 Feb 2020

Cappaert, D., McCullough, D. G., Poland, T. M., & Siegert, N. W. (2005). Emerald ash borer in North America a research and regulatory challenge. *American Entomologist*, *51*, 152–165. https://doi.org/10.1093/ae/51.3.152

Cobeldick, S. (2020). *ColorBrewer: Attractive and distinctive colormaps*. GitHub. https://www.github.com/DrosteEffect/BrewerMap. Retrieved February 24, 2020

Coker, T. L. R., Rozsypálek, J., Edwards, A., Harwood, T. P., Butfoy, L., & Buggs, R. J. A. (2019). Estimating mortality rates of European ash (*Fraxinus excelsior*) under the ash dieback (*Hymenoscyphus fraxineus*) epidemic. *Plants*, *People*, *Planet*, *1*, 48–58. https://doi.org/10.1002/ppp3.11

Dearborn, K. W., Macquarrie, C. J. K., & Inward, D. J. G. (2018). Emerald ash borer development rates and modelling for potentially invaded regions of Canada and Britain. In P. Mayer (Ed.), *Preparing Europe for invasion by the beetles emerald ash borer and bronze birch borer, two major tree-killing pests*. 55 pp. https://bfw.ac.at/cms_stamm/050/PDF/prepsys_abstracts.pdf

Donovan, G. H., Butry, D. T., Michael, Y. L., Prestemon, J. P., Liebhold, A. M., Gatziolis, D., & Mao, M. Y. (2013). The relationship between trees and human health: Evidence from the spread of the emerald ash borer. *American Journal of Preventive Medicine*, *44*, 139–145. https://doi.org/10.1016/j.amepre.2012.09.066

Duart, S. A. D. (2013). *Characterizing prepupal diapause and adult emergence phenology of emerald ash borer*. MSc thesis, The Ohio State University.

Gandhi, K. J. K., & Herms, D. A. (2010). Direct and indirect effects of alien insect herbivores on ecological processes and interactions in forests of eastern North America. *Biological Invasions*, *12*, 389–405. https://doi.org/10.1007/s10530-009-9627-9

Greene, C. A., Thirumalai, K., Kearney, K. A., Delgado, J. M., Schwanghart, W., Wolfenbarger, N. S., Thyng, K. M., Gwyther, D. E., Gardner, A. S., & Blankenship, D. D. (2019). The Climate Data Toolbox for MATLAB. *Geochemistry*, *Geophysics*, *Geosystems*, *20*, 3774–3781. https://doi.org/10.1029/2019GC008392

Haack, R. A., Jendek, E., Lui, H., & Ye, H. (2002). The emerald ash borer: A new exotic pest in North America. *Newsletter of the Michigan Entomological Society*, *47*, 1–5.

Herms, D. A., & McCullough, D. G. (2014). Emerald ash borer invasion of North America: History, biology, ecology, impacts, and management. *Annual Review of Entomology*, *59*, 13–30. https://doi.org/10.1146/annurev-ento-011613-162051

Iverson, L. R., Prasad, A., Bossenbroek, J., Sydnor, D., & Schwartz, M. W. (2010). Modeling potential movements of the emerald ash borer: the model framework. *Advances in Threat Assessment and their Application to Forest and Rangeland Management*, *1*, 581–597.

Jacobi, W. R., Hardin, J. G., Goodrich, B. A., & Cleaver, C. M. (2012). Retail firewood can transport live tree pests. *Journal of Economic Entomology*, *105*, 1645–1658. https://doi.org/10.1603/ec12069

Jones, M. I., Gould, J. R., Mahon, H. J., & Fierke, M. K. (2019). Phenology of emerald ash borer (Coleoptera: Buprestidae) and its introduced larval parasitoids in the Northeastern United States. *Journal of Economic Entomology*, *2007*, 1–11. https://doi.org/10.1093/jee/toz304

Kondo, M. C., Han, S. H., Donovan, G. H., & MacDonald, J. M. (2017). The association between urban trees and crime: Evidence from the spread of the emerald ash borer in Cincinnati. *Landscape and Urban Planning*, *157*, 193–199. https://doi.org/10.1016/j.landurbplan.2016.07.003

Kovacs, K. F., Haight, R. G., McCullough, D. G., Mercader, R. J., Siegert, N. W., & Liebhold, A. M. (2010). Cost of potential emerald ash borer damage in U.S. communities, 2009–19. *Ecological Economics*, *69*, 569–578. https://doi.org/10.1016/j.ecolecon.2009.09.004

Kovacs, K. F., Haight, R. G., Mercader, R. J., & McCullough, D. G. (2014). A bioeconomic analysis of an emerald ash borer invasion of an urban forest with multiple jurisdictions. *Resource and Energy Economics*, *36*(1), 270–289. https://doi.org/10.1016/j.reseneeco.2013.04.008

Lyons, D. B., & Jones, G. C. (2005). The biology and phenology of the emerald ash borer. In K. W. Gottschalk (Ed.), *Proceedings*, *16th U.S. Department of Agriculture interagency research forum on gypsy moth and other invasive species*, (pp. 62–63). Annapolis, MD. Gen. Tech. Rep. NE-337. https://doi.org/10.2737/NE-GTR-337

Lyttek, E., Lal, P., Nieddu, G., Forgoston, E., & Wieczerak, T. (2019). Modeling *Agrilus planipennis* F. (Coleoptera: Buprestidae) spread in New Jersey. *Journal of Economic Entomology*, *112*(5), 2482–2488. https://doi.org/10.1093/jee/toz122

Maskell, L., Henrys, P., Norton, L., Smart, S., & Wood, C. (2013). *Distribution of ash trees (*Fraxinus excelsior*) in countryside survey data*. Center for Ecology and Hydrology.

McCullough, D. G. (2020). Challenges, tactics and integrated management of emerald ash borer in North America. *Forestry*, *93*, 197–211. https://doi.org/10.1093/forestry/cpz049

McCullough, D. G., & Mercader, R. J. (2012). Evaluation of potential strategies to SLow Ash Mortality (SLAM) caused by emerald ash borer (*Agrilus planipennis*): SLAM in an urban forest. *International Journal of Pest Management*, *58*(1), 9–23. https://doi.org/10.1080/09670874.2011.637138

Mercader, R. J., McCullough, D. G., Storer, A. J., Bedford, J. M., Heyd, R., Siegert, N. W., Katovich, S., & Poland, T. M. (2016). Estimating local spread of recently established emerald ash borer, *Agrilus planipennis*, infestations and the potential to influence it with a systemic insecticide and girdled ash trees. *Forest Ecology and Management*, *366*, 87–97. https://doi.org/10.1016/j.foreco.2016.02.005

Mercader, R. J., Siegert, N. W., Liebhold, A. M., & McCullough, D. G. (2011). Simulating the effectiveness of three potential management options to slow the spread of emerald ash borer (*Agrilus planipennis*) populations in localized outlier sites. *Canadian Journal of Forest Research*, *41*, 254–264. https://doi.org/10.1139/X10-201

Muirhead, J. R., Leung, B., van Overdijk, C., Kelly, D. W., Nandakumar, K., Marchant, K. R., & MacIsaac, H. J. (2006). Modelling local and long-distance dispersal of invasive emerald ash borer *Agrilus planipennis*

(Coleoptera) in North America. *Diversity and Distributions*, *12*(1), 71–79. https://doi.org/10.1111/j.1366-9516.2006.00218.x

Musolin, D. L., Selikhovkin, A. V., Shabunin, D. A., Zviagintsev, V. B., & Baranchikov, Y. N. (2017). Between ash dieback and emerald ash borer: Two Asian invaders in Russia and the future of ash in Europe. *Baltic Forestry*, *23*, 316–333.

Orlova-Bienkowskaja, M. J., & Bieńkowski, A. O. (2016). The life cycle of the emerald ash borer *Agrilus planipennis* in European Russia and comparisons with its life cycles in Asia and North America. *Agricultural and Forest Entomology*, *18*, 182–188. https://doi.org/10.1111/afe.12140

Orlova-Bienkowskaja, M. J., & Bieńkowski, A. O. (2018). Modeling long-distance dispersal of emerald ash borer in European Russia and prognosis of spread of this pest to neighboring countries within next 5 years. *Ecology and Evolution*, *8*, 9295–9304. https://doi.org/10.1002/ece3.4437

Orlova-Bienkowskaja, M. J., Drogvalenko, A. N., Zabaluev, I. A., Sazhnev, A. S., Peregudova, E. Y., Mazurov, S. G., Komarov, E. V., Struchaev, V. V., Martynov, V. V., Nikulina, T. V., & Bieńkowski, A. O. (2020). Current range of *Agrilus planipennis* Fairmaire, an alien pest of ash trees, in European Russia and Ukraine. *Annals of Forest Science*, *77*. https://doi.org/10.1007/s13595-020-0930-z

Poland, T. M., & McCullough, D. G. (2006). Emerald ash borer: Invasion of the urban forest and the threat to North America's ash resource. *Journal of Forestry*, *104*, 118–124. https://doi.org/10.1093/jof/104.3.118

Poland, T. M., McCullough, D. G., & Anulewicz, A. C. (2011). Evaluation of double-decker traps for emerald ash borer (Coleoptera: Buprestidae). *Journal of Economic Entomology*, *104*, 517–531. https://doi.org/10.1603/ec10254

Prasad, A., Iverson, L. R., Peters, M. P., Bossenbroek, J., Matthews, S. N., Sydnor, T. D., & Schwartz, M. W. (2010). Modeling the invasive emerald ash borer risk of spread using a spatially explicit cellular model. *Landscape Ecology*, *25*, 353–369. https://doi.org/10.1007/s10980-009-9434-9

Saunders, D. (2020). Insect photoperiodism: Seasonal development on a revolving planet. *European Journal of Entomology*, *117*, 328–342. https://doi.org/10.14411/eje.2020.038

Short, M. T., Chase, K. D., Feeley, T. E., Kees, A. M., Wittman, J. T., & Aukema, B. H. (2020). Rail transport as a vector of emerald ash borer. *Agricultural and Forest Entomology*, *22*, 92–97. https://doi.org/10.1111/afe.12360

Showalter, D. N., Saville, R. J., Orton, E. S., & Brown, J. K. M. (2020). Resistance of European ash (*Fraxinus excelsior*) saplings to larval feeding by the emerald ash borer (*Agrilus planipennis*). *Plants, People, Planet*, *2*, 41–46. https://doi.org/10.1002/ppp3.10077

Siegert, N. W., McCullough, D. G., Liebhold, A. M., & Telewski, F. W. (2014). Dendrochronological reconstruction of the epicentre and early spread of emerald ash borer in North America. *Diversity and Distributions*, *20*, 847–858. https://doi.org/10.1111/ddi.12212

Siegert, N. W., Mercader, R. J., & McCullough, D. G. (2015). Spread and dispersal of emerald ash borer (Coleoptera: Buprestidae): estimating the spatial dynamics of a difficult-to-detect invasive forest pest. *The Canadian Entomologist*, *147*(3), 338–348. https://doi.org/10.4039/tce.2015.11

Straw, N. A., Williams, D. T., Kulinich, O., & Gninenko, Y. I. (2013). Distribution, impact and rate of spread of emerald ash borer *Agrilus planipennis* (Coleoptera: Buprestidae) in the Moscow region of Russia. *Forestry*, *86*, 515–522. https://doi.org/10.1093/forestry/cpt031

Taylor, R. A. J., Bauer, L. S., Poland, T. M., & Windell, K. N. (2010). Flight performance of *Agrilus planipennis* (Coleoptera: Buprestidae) on a flight mill and in free flight. *Journal of Insect Behavior*, *23*, 128–148. https://doi.org/10.1007/s10905-010-9202-3

Tluczek, A. R., McCullough, D. G., & Poland, T. M. (2011). Influence of host stress on emerald ash borer (Coleoptera: Buprestidae) adult density, development, and distribution in Fraxinus pennsylvanica trees. *Environmental Entomology*, *40*(2), 357–366. https://doi.org/10.1603/EN10219

Valenta, V., Moser, D., Kapeller, S., & Essl, F. (2017). A new forest pest in Europe: A review of emerald ash borer (*Agrilus planipennis*) invasion. *Journal of Applied Entomology*, *141*, 507–526. https://doi.org/10.1111/jen.12369

Wang, X.-Y., Yang, Z.-Q., Gould, J. R., & Liu, E.-S. (2010). The biology and ecology of the emerald ash borer, *Agrilus planipennis*, in China. *Journal of Insect Science*, *10*, 1–23. https://doi.org/10.1673/031.010.12801

Ward, S. F., Fei, S., & Liebhold, A. M. (2020). Temporal dynamics and drivers of landscape-level spread by emerald ash borer. *Journal of Applied Ecology*, *57*, 1020–1030. https://doi.org/10.1111/1365-2664.13613

Waters, L. (2016). *Summary results of the domestic wood use survey*. UK Gov. Rep. www.gov.uk/government/uploads/system/uploads/attachment_data/file/517572/Summary_results_of_the_domestic_wood_use_survey_.pdf

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